

MESOZOIC DISPERSAL OF TERRESTRIAL FAUNAS AROUND THE SOUTHERN END OF THE WORLD

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Summary. — This paper considered the relationship between late Mesozoic-early Cenozoic paleogeography and the evolution and dispersal of vertebrates in the Southern Hemisphere. The major points raised are as follows :

1. There is now sufficient evidence from geology to show that the separations of the Gondwana continents took place in the Late Cretaceous-early Cenozoic. The final land connection between Africa and South America was about 90 m. y. ago in the Late Cretaceous. New Zealand separated from West Antarctica about 80 m. y. ago. Australia moved northward from East Antarctica sometime in the Eocene, about 43-45 m. y. ago. Finally, the Andean Cordillera-Antarctic Peninsula mountain chain fragmented to form the Scotia Arc most likely in the early Cenozoic.

2. Biogeographic hypotheses should be based, whenever possible, on a prior phyletic analysis. The main goal then is to construct hypotheses about the location of ancestors. In so doing the center of origin of a group can be shown to be the place where the phyletically primitive taxa are located.

3. South America and Africa share a large vertebrate fauna that most probably evolved from a common fauna inhabiting a once-united supercontinent. This fauna includes numerous fishes (catfishes, characids, cichlids), amphibians (pipids, bufonids, leptodactylids, microhylids), reptiles (teiids, lacertids, boas-pythons, geckos), birds (rheas-ostriches), but apparently no mammals.

4. South America and Australia also share a fauna that must have dispersed through East Antarctica, but it is less diverse than that characterizing the South America-Africa interchange. Included here are fishes (probably osteoglossomorphs), amphibians (leptodactylids), birds (cassowaries-emus, megapodes, probably others), and mammals (monotremes, marsupials).

5. Of all the southern continents New Zealand shows the least diverse vertebrate fauna. Still, some elements probably arrived from South America via West Antarctica : kielpelmatid frogs, sphenodontid lizards, and moas-kiwis.

6. There is no evidence suggesting predrift interchange of vertebrates between Africa and Australia (via Antarctica) or between Australia and New Zealand.

7. The paucity of southern vertebrate elements on New Zealand as compared to Australia can be accounted for by (a) the earlier separation of New Zealand, and (b) the archipelagic nature of the dispersal route through West Antarctica.

8. Invertebrates appear to show similar patterns of dispersal as the vertebrates.

9. The relative ages of the sister-group connections of each fauna appear to be related, to some degree, to the times of separation and therefore to the length of isolation. Africa and South America, in general, share sister-groups of family rank or higher, as do also New Zealand and South America. The faunas of Australia and South America are separated not only at the family-rank but also at subfamily and generic rank.

10. The final separations of the Gondwana continents undoubtedly did much to increase taxonomic diversity by facilitating isolation and subsequent differentiation of the faunas.

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INTRODUCTION

The problem of Southern Hemisphere biogeography and its relationship to the paleogeographic history of the southern continents has interested biologists for many years (see, for example, Hedley, 1912; Harrison, 1924; Olivier, 1925; Wittmann, 1934, 1935; Simpson, 1940; Mayr, 1952; Darlington, 1957, 1965; Fleming, 1962, 1963; Knox, 1963; Brundin, 1965, 1966, 1970; Reig, 1968; Gaskin, 1970; Keast, 1971, 1973; Raven and Axelrod, 1972; and many papers on specific groups, some of which are cited below). Because great controversy continually surrounded the geological evidence for and against continental drift, the first half of this century saw vigorous debate among biologists as to the usefulness of their data in shedding light on the different geological hypotheses, and also the extent to which geological evidence explained the distribution of southern biota. Unfortunately, the biological data themselves were often interpreted in light of preconceptions about earth history. As a consequence, the majority of workers seemed to find support for stable continents in the biological data, and many vehemently denied the possibility of continental drift. Indeed, the stable continent tradition still influences some biogeographers as evidenced by statements that if drift occurred, it was too far in the past to influence the distribution of most of the Recent vertebrates (e.g., Darlington, 1964, 1965, 1970; Mayr, 1972).

The last ten years have seen a remarkable advance in our knowledge of the earth. For nearly all geologists, continental drift is now an accepted fact and an important facet of what is termed the New Global Tectonics (Morgan, 1968; Dickinson, 1971; Dewey, 1972; McKenzie, 1972). Our knowledge of past continental positions and times of separation and drift is rapidly increasing and is certain to become more definitive in the next few years. It is also increasingly evident that plate tectonics will have an important impact on biological science, especially evolutionary biology (Jardine and McKenzie, 1972; Valentine and Moores, 1972; Axelrod, 1972; Axelrod and Raven, 1972; McKenna, 1972). For the biologist interested in the biogeography of the Southern Hemisphere, perhaps the most important aspect of these new geological data is that we can now be fairly certain that most of the southern continents maintained interconnections well into the Cretaceous (evidence reviewed below). This means, of course, that most families of Recent vertebrates, or their immediate ancestors, were in existence when it was possible to disperse overland among the southern continents.

Most previous discussions of Southern Hemisphere biogeography and continental drift have emphasized invertebrate groups or plants (see many of the papers cited above). In general, those papers treating the problem of vertebrate distribution either have tended to argue against or at least questioned the importance of drift for the dispersal of most of the Recent vertebrate families (e.g., Simpson, 1940; Darlington, 1965; Keast, 1971: 355-356; Mayr, 1972). In this paper I want to review some of the evidence which supports the thesis that continental drift was of paramount significance in determining the early patterns of evolution and dispersal of Recent vertebrates (see also Cracraft, in press a). Emphasis here will be on the terrestrial vertebrate faunas, but brief mention also will be given to fresh-water fishes and, in the discussion, to invertebrates because of their usefulness in helping us understand some of the factors influencing the formation of the vertebrate patterns. I have presented elsewhere a detailed discussion of avian biogeographic patterns (1973 a) and of some vertebrate patterns in the Old World tropics, that is, tropical Africa and Eurasia (1973 b), thus these subjects will not be considered in detail here.

SOUTHERN HEMISPHERE PALEOGEOGRAPHY

The geological literature bearing on the reconstruction and breakup of Gondwanaland has been reviewed by several workers (Smith and Hallam, 1970; Keast, 1971; Elliot, 1972; Cracraft, 1973 a), and hence this discussion is restricted to the principal conclusions and most probable hypotheses of Mesozoic paleogeography.

A predrift reconstruction of Gondwanaland is depicted in Fig. 1. Constraints are placed on possible reconstructions by several continental fits which are reasonably well documented. First, the fit between South America and Africa is accepted by all workers and is supported by a wealth of geological data (Bullard, *et al.*, 1965; Hurley and Rand, 1969; Allard and Hurst, 1969; Smith and Hallam, 1970; Le Pichon and Hayes, 1971). Second, it is now evident that the Andean Cordillera-Antarctic Peninsula connection was essentially linear prior to breakup and formation of the Scotia Arc (Dalziel and Elliot, 1971; Elliot, 1972). This places important constraints on paleogeographic models which were not incorporated by previous workers (e.g., Smith and Hallam, 1970; Dietz and Holden, 1970; Veevers, *et al.*, 1971). Third, the fit between Australia and East Antarctica can be justified by considerable data (Sproll and Dietz, 1969; Smith and Hallam, 1970).



FIG. 1. — A reconstruction of Gondwanaland prior to breakup, about 155 m.y. ago. South America and Antarctica are fitted according to Dalziel and Elliot (1971). Australasia is fitted according to Griffiths (1971). Following other models [e.g., Smith and Hallam, 1970], Madagascar is fitted to Kenya, but it may have been attached to Mozambique (see text).

The positions of the remaining continents can now be considered relative to the above three "fixed" intercontinental ligations. The linear arrangement of the Andean Cordillera-Antarctic Peninsula calls for adjustments in the fit of Africa and Antarctica proposed by Dietz and Sproll (1970). If it is assumed that Africa and Antarctica were in contact prior to breakup, then the South America-Antarctica reconstruction of Dalziel and Elliot (1971) requires that Madagascar fit northward against Kenya rather than have a more southerly fit next to Mozambique. With Madagascar adjacent to Mozambique, the former continent would seem to lie between Africa and Antarctica and thus preclude their contact (see Cracraft, 1973 a, for details). The fit of Madagascar against Kenya is said to be supported by some geological evidence (Smith and Hallam, 1970; Helzler and Burroughs, 1971), but these data are questioned by some workers. Flores (1970) has presented considerable stratigraphic data arguing for a fit of Madagascar to Mozambique. The exact location of the Madagascar-Africa fit is not critical to the biogeographic problems discussed in this paper.

In this reconstruction of Gondwanaland I have chosen to place India with its eastern margin against Antarctica and with its western edge against Madagascar and Africa. This follows, in general,

previous workers (e.g., Smith and Hallam, 1970; Dietz and Holden, 1970) but for somewhat different reasons. The fit of India against Australia advocated by Veevers, *et al.* (1971) seems unlikely at the present time, because the probable geological events associated with the breakup of India from Antarctica and Madagascar cannot be easily reconciled with their model (see Cracraft, 1973 a, and below, for details).

The final continent to be fitted to Gondwanaland is New Zealand. Using more complete bathymetric and geophysical information, Griffiths (1971) has placed the Campbell Plateau and the Chatham Rise against West Antarctica and the Ross Sea (Fig. 2). Thus, the Lord Howe Rise and Norfolk Ridge are interposed between New Zealand and Australia. This model, along with the Antarctica-Australia fit noted above, fairly nicely explains the complex geology of the Australasian region and aligns the complex orogenic belts and geosynclines of this region (Griffiths, 1971, fig. 4), although many details are yet to be worked out.

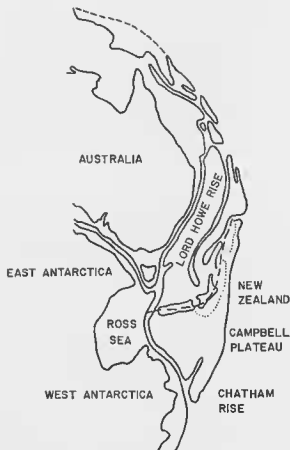


Fig. 2. — A reconstruction of Australasia prior to breakup, about 80 m.y. ago. After Griffiths (1971). See text.

The following description of the breakup and dispersal of Gondwanaland is based, when available, on several kinds of evidence. For determining the time of rifting and initial breakup between continents, I have used (1) dated volcanism, (2) marine sedimentation along continental margins, and (3) timing of changes in faunal similarities and dissimilarities. Movements of continents have been plotted using magnetic anomaly patterns on the ocean floor and paleomagnetism. However, where possible, I have used only seafloor spreading data as being more reliable and informative than paleomagnetic studies.

In the western part of Gondwanaland breakup between Africa and South America began in the south and moved northward. Dated core samples suggest that the South Atlantic began to open at about

or somewhat prior to the early Cretaceous, approximately 130 m.y. ago (Maxwell, *et al.*, 1970). This accords well with the 140 m.y. date extrapolated from sea floor spreading data (Le Pichon and Hayes, 1971). However, final separation of Africa and South America did not take place until sometime later. The first salt deposits indicating marine ingression in the Sergipe basin of Brazil and Gabon basin of Africa were formed in the late Aptian, about 110 m.y. ago (Allerd and Hurst, 1960). Final separation of the subaerial land masses probably did not take place until the lower Turonian on the basis of the geology of the Benue Trough (Wright, 1968) and invertebrate biostratigraphy (Reyment, 1969; Reyment and Tait, 1972). Thus, some land connection was still present about 90 m.y. ago. The above data are also consistent with the final separation of the continental crust of the South American and African plates about 80 m.y. ago as evidenced by a shift in their pole of rotation (Le Pichon and Hayes, 1971).

There is now fairly good evidence that the Andean Cordillera-Antarctic Peninsula interconnection did not begin to fragment to form the Scotia Arc until the very latest Cretaceous or early Tertiary, and the latter time is more probable (Barker, 1970; Hamilton, 1967; Dalziel and Elliot, 1971).

Africa and Antarctica probably separated sometime between the middle Jurassic and middle Cretaceous although the earlier time is likely to be more nearly correct (Le Pichon and Heirtzler, 1968; Smith and Hallam, 1970; McElhinny, 1970). Dingle and Klinger (1971) have noted that the oldest marine rocks at the southern tip of Africa are of late Jurassic age.

As Africa and Antarctica moved further apart, breakup soon had to involve India and Madagascar. The various models for the early evolution of the southwestern part of the Indian Ocean are very complex and cannot be reviewed here (Cracraft, 1973 a). The hypothesis accepted here is that India separated from Antarctica prior to breakup from Madagascar/Africa. The rifting and possible breakup of India and Antarctica is perhaps correlated with the extrusion of the Rajmahal Traps which are dated at about 100 m.y. (McDougall and McElhinny, 1970; McElhinny, 1970) and with a Cenomanian marine transgression along the Coromandel coast of southeastern India (Smith and Hallam, 1970).

The breakup of India/Antarctica in about the early late Cretaceous was probably followed by separation of Madagascar and Africa. No magnetic anomalies are present in the Mozambique Channel to suggest the time of drift between these two continents (Heirtzler and Burroughs, 1971), but Cretaceous volcanism and faunal evidence suggest a Late Cretaceous time of separation (Smith and Hallam, 1970: 143; Keast, 1971). Flores (1970) envisions a Cretaceous separation of Madagascar from the Mozambique coast. In the Late Cretaceous, or perhaps slightly later in the very earliest Tertiary, India apparently separated from Madagascar and the Seychelles. The evidence for this is paleomagnetic (McElhinny, 1970), the Late Cretaceous-early Tertiary extrusion of the Deccan Traps in India (Davies, 1968), and sea floor spreading (Le Pichon and Heirtzler, 1968; Fisher, *et al.*, 1971), although it must be stressed that there are no magnetic anomalies between India and Madagascar definitely showing this to be true. McKenzie and Selater (1971) have discussed the evolution of the Indian Ocean based on magnetic anomalies. Unfortunately they are unable to determine India's position prior to 75 m.y. ago.

The timing of breakup and drift of eastern Gondwanaland is based mainly on sea floor spreading data. New Zealand separated from West Antarctica by spreading away from the Pacific-Antarctic Ridge beginning in the Late Cretaceous, about 80 m.y. ago (Pitman, *et al.*, 1968; Griffiths and Varne, 1972). Considerable northward drift of New Zealand had taken place prior to breakup of Australia and Antarctica (Fig. 3). Australia began to move northward in the middle to late Eocene (43-45 m.y. ago) as shown by the presence of anomaly 18 along the Australian continental margin (Le Pichon and Heirtzler, 1968; Le Pichon, 1968). This also correlates well with extensive Eocene marine sedimentation along the southern coast of Australia (Jones, 1971). Recent magnetic anomaly data from the Tasman Sea indicate sea floor spreading between the Lord Howe Rise and Australia from about 80 to 60 m.y. ago (Hayes and Ringis, 1972; Hayes pers. comm.), and in general this new information is consistent with the model (Fig. 3) of Griffiths and Varne (1972) although the details are somewhat different.

The above discussion of Gondwanaland paleogeography is summarized in Fig. 4. I emphasize here that the figure only attempts to show the most probable times of continental separation as we

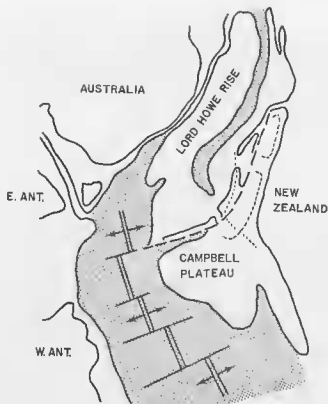


FIG. 3. — A reconstruction of the southwest Pacific at about 60 m.y. Stippled area represents ocean floor that has been formed between 60-80 m.y. ago. After Griffiths and Varne (1972).

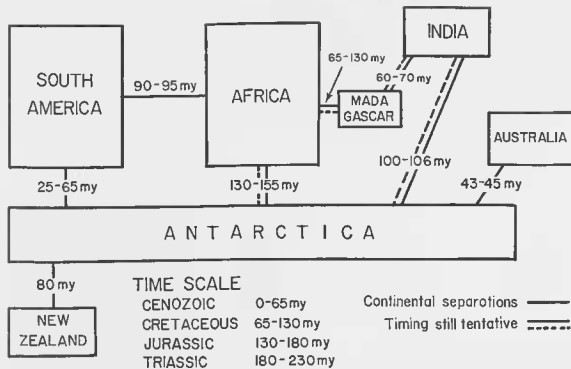


FIG. 4. — A summary schematic representation of the breakup of Gondwanaland to show approximate times of separation of the various continents. Those separations that are particularly uncertain are noted by the dashed line. See text and Smith and Hallam (1970) and Cracraft (1973a) for detailed data.

currently understand them. Some of the dates will undoubtedly have to be revised as new observations are made. The important point for biogeographers is that geological evidence currently indicates that many of the southern continents were still connected to one another in the Late Cretaceous. Since many families of Recent vertebrates had arisen by then, late Mesozoic paleogeography becomes an important factor in their evolution and dispersal.

BIOGEOGRAPHIC THEORY

Most biogeographers subscribe to the general belief that an understanding of phylogenetic relationships is essential for meaningful biogeographic analysis. However, only a relatively small number of workers have attempted to formalize this relationship between phylogeny and biogeography into a set of working methods. Most of these have been followers of the school of systematics termed "phylogenetic systematics" or "cladistics" (Hennig, 1960, 1966; Brundin, 1966, 1972; Nelson, 1963a; Cracraft, 1972 a, 1973 a).

A principle goal of biogeography should be the construction of hypotheses about the location of ancestral species. Such a procedure would necessarily follow a phyletic analysis and would then permit statements to be made about centers of origin and pathways of dispersal. The above systematic theory implies, of course, that phylogenetically primitive species will in general be located near the center of origin of the group in question, whereas more derivative or advanced taxa will tend to be distributed peripherally to the center of origin. Some biogeographers (e.g., Darlington, 1957, 1970) reject this reasoning and in so doing essentially reject the role of phylogeny in biogeography. Biogeographic theory is meaningful only when it is based on a cladistic approach to relationships. Intuitively, if primitive and derived taxa are not distributed in some manner reflecting phylogeny, it will be impossible to reconstruct the biogeographic history of that group. Hence, biogeography must rely on phylogeny. Darlington (1957) and some other workers have the belief that present-day diversity gradients are useful in recognizing centers of origin. This assumption loses much of its significance not only in theory but also when it is realized these gradients may only reflect events of the last few million years. On the contrary, the major features of most vertebrate distribution patterns were probably established and modified by paleogeographic and paleoclimatic factors very different from those of the Plio-Pleistocene.

The biogeographic theory discussed by the above-mentioned phylogeneticists will not be elaborated on here. Rather, I want to point out several specific approaches derived from their work that will be used to analyse the biogeographic patterns discussed below. First, attempts will be made to document sister-group relationships (Hennig, 1966), that is, the identification of each taxon's closest relative, for various taxa on the different southern continents. These sister-groups sometimes involve interfamilial relationships (e.g., several lizard families, ratite birds) or they may be for taxa within a single family (pipid and leptodactylid frogs).

A problem exists in that the inter- and intrafamilial affinities of many vertebrate and invertebrate families are still poorly known. Even if the intergeneric cladistic affinities of a family have not yet been determined, it is frequently possible for systematists to recognize the most primitive and most advanced genera. Such information can sometimes be extremely valuable in determining the most likely pathways of dispersal and in facilitating recognition of whether a group is primarily southern or northern. For example, within a family that is distributed over North, Central, and South America, it may be possible to outline the general cladistic relationships of some of the genera. If the most primitive taxa of a family are in South America and the most derivative in northern Central America and/or North America, it is likely that the family will have its sister-group in South America, Africa, or Australasia (see Cracraft, 1973 a, in press a; and Brundin, 1966; for a fuller discussion). Such a pattern is common for many vertebrate families (see below). Likewise, if the evolutionary trends are reversed, the sister-group for the family will probably be North American or Eurasian. It can be concluded from this discussion that the results of systematists studying groups even from a limited geographic area can have profound significance for those workers examining the influences of continental drift (e.g., see the papers of Myers, 1966; Duellman, 1970).

The above theory is also powerful in that biogeographic hypotheses can themselves be tested by future phyletic analyses. The phylogenetic relationships of many vertebrate taxa are essentially unknown, and it may be possible to suggest one or more biogeographic hypotheses to explain their distribution. Subsequent phylogenetic analyses can then be used to reject certain of the biogeographic hypotheses. In this way, it should be possible to make biogeography much more accountable scientifically than has been done in the past by eliminating unnecessary intuition.

FAUNAL AFFINITIES AMONG THE SOUTHERN CONTINENTS

This section discusses those faunal similarities among the vertebrates of the southern continents which seem to be the result of predrift land connections. Little attention is given to similarities considered to have formed after breakup when the continents were either in approximately their present positions or at least separated by significant water barriers. In the absence of an adequate knowledge of cladistic relationships, it obviously will be difficult to decide whether a particular distribution is sufficiently old to be considered in terms of continental drift. Fossils are of some help and in addition, like most workers, I have tended to assume that the higher the rank of the taxon in question, the older is that taxon (for comparisons within a class, this is probably valid). Fortunately, too, the fossil record of vertebrates is becoming better known on each continent, and more and more records are showing that Recent genera and families are more ancient than previously realized. This new paleontological information gives us an additional basis on which to estimate the possible minimal age of a particular group. In the long run, however, it will be a knowledge of the cladistic relationships that will allow us to reconstruct biogeographical history.

This paper is an attempt to look at general patterns of vertebrates on southern continents. Because of space limitations, it is not possible to discuss the systematic evidence for each group in the detail I would prefer. However, I have attempted to pay closer attention to those taxa which are particularly controversial. Additionally, I have noted the sources for my conclusions in several tables even though I may not discuss those sources extensively in the text. Many of these workers have not stated outright the conclusions I have seemingly cited them for, but nevertheless in many cases they provided useful data for my zoogeographic hypotheses (e.g., such as the location of primitive and advanced taxa).

TABLE 1. — Vertebrate taxa showing probable sister-group relationships between Africa and South America¹

Taxon in Africa	Taxon in South America	Source of systematic data ²
<i>Fresh-water Fishes</i>		
Lepidosirenidae (<i>Protopterus</i>)	Lepidosirenidae (<i>Lepidosiren</i>)	a
Osteoglossidae (<i>Heterotis</i>)	Osteoglossidae (<i>Arapaima</i>)	a, b
Characidae	Characidae	c
Siluriformes	Siluriformes	c, d
Nandidae	Nandidae	e, f
Cichlidae	Cichlidae	g
Cyprinodontidae	Cyprinodontidae	h

1. Includes only Recent families.

2. Abbreviations : a, Patterson, in press ; b, G. J. Nelson, 1969b ; c, Regan, 1922 ; d, Gosline, 1944 ; e, Liem, 1970 ; f, K. Liem, pers. comm. ; g, Eigenmann, 1909 ; h, Myers, 1938 ; i, Estes and Wake, 1972 ; j, Lynch, 1971 ; k, Trueth, 1971 ; l, McDiarmid, 1971 ; m, C. Nelson and Cuellar, 1968 ; n, C. Nelson, 1972 ; o, Carvalho, 1954 ; p, Blair, 1972 ; q, Camp, 1923 ; r, Kluge, 1967 ; s, Gorman, 1970 ; t, Underwood, pers. comm. ; u, Cracraft, 1973a ; v, Cracraft, in press b.

Amphibians

Caeciliidae	Caeciliidae	i
Pipidae	Pipidae	—
Leptodactylidae	Leptodactylidae	j
Bufoinidae	Bufoinidae (Atelopodidae)	q, k, l, p
Microhylidae	Microhylidae	m, n, o

Reptiles

Agamidae	Iguanidae	q
Gekkoninae	Gekkoninae	r
Lacertidae	Teiidae	q, s
Pythoninae	Boinae	t

Birds

Struthioninae	Rheinae	u, v
Some other suboscines ¹	Eurylaimidae	u

Mammals

Nona ²	—	—
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SOUTH AMERICA-AFRICA

Of all the southern continents Africa and South America share more of the Mesozoic Gondwanaland Element than do any other two continents (Table 1). This is to be expected considering the long history of this intercontinental ligation and the general similarities in climate that presumably prevailed in the two regions prior to breakup.

That the South American fresh-water fish fauna is predominately Gondwana in origin is supported by considerable evidence (Eigenmann, 1909; Regan, 1922; Gosline, 1944, in press; Myers, 1967; Gery, 1969; Patterson, in press). Nearly all of the major groups of fishes in South America are shared with Africa (Darlington, 1957). Evolutionary patterns within tropical American taxa fully support this conclusion since the fish fauna of Central America is almost certainly derived from the south and not the north (Myers, 1966). As this latter author notes (1967: 772): "the derivation of the excessively rich South American freshwater fish fauna, especially the cypriniform characoids, from Asian immigrants which filtered through the North and Central American faunas without leaving a trace (Darlington, 1957), cannot be seriously entertained." However, it is also no longer necessary to push back the origin of these South American groups to the Triassic or Jurassic (Myers, 1967), since an Early to Middle Cretaceous (even Late Cretaceous) age would be more than satisfactory (see above). Freshwater fishes from the lower Cretaceous of Brazil and equatorial Africa are quite similar (Patterson, in press), which suggests there may have been a continuous connection at that time. Those groups of fresh-water fishes that were part of a fauna common to South America and Africa include the lung-fish Lepidosirenidae (*Protopterus*, *Lepidosiren*), osteoglossomorphs (especially the Heterotinae), siluriform catfishes, Characidae, Nandidae, Cichlidae, and others (Table 1).

The amphibians also provide a number of examples, which strongly support a former land connection between South America and Africa (Cracraft, 1973 b). The primitive Caeciliidae are distributed within the tropics of the world, and there is no evidence suggesting northern dispersal. A recently described genus from the Paleocene of Brazil shows some similarities to the African genus

1. Specific group unknown; interrelationships very poorly known.

2. Prototherian or metatherian link not yet known; no evidence for any eutherian taxa using direct land connections (see text).

Geotrypetes (Estes and Wake, 1972). Until intergeneric relationships are known, little specific can be said about caecilians. The Pipidae are a primitive frog family confined to Africa and South America and thus were very probably a part of the Gondwanaland fauna. The leptodactylids have had an extensive radiation in the South American tropics, and their evolutionary patterns indicate a definite dispersal from South America into Central America (Lynch, 1971). Africa has an endemic leptodactylid subfamily, the Heleophryinae, and the family itself probably had its early evolution in Africa (Lynch, 1971). There are important similarities between the South American "atelopodine" bufonids in South America and the more "typical" bufonid genera in Africa (Trueb, 1971). Blair (1972) maintains that the genus *Bufo* originated in South America and spread northward; if true, this would support a Gondwana origin for the family. The Microhylidae are another probable Gondwanaland family, but unfortunately much remains to be learned about their phyletic relationships. Within the New World, primitive microhylids are in South America and the North American forms are probably derived from them (Carvalho, 1954). The Central American microhylids were apparently derived from South America (Savage, 1966). Nelson and Cuellar (1968) and C. Nelson (1972) have argued that the North American genera do not seem closely related to the Asiatic generic complex that includes *Microhyla* (unfortunately, because of a typographical error, the opposite conclusion was implied in Cracraft, 1973 b).

South America and Africa are the only southern continents for which there is fairly good evidence of a Gondwanaland history for contemporary reptile families. The Iguanidae and Agamidae are two closely related families with complementary distributions (Camp, 1923), the iguanids in the New World and the agamids in the Old. That iguanids once had an African distribution seems certain because of undoubted forms on Madagascar. Presumably, primitive iguanids were never very abundant in Africa and were replaced by their close relatives, the agamids and chamaeleontids. The presence of iguanids in the Late Cretaceous of South America attests to their age (Estes, 1970), and dispersal patterns within the New World have been from the south northward (Savage, 1966). Another complementary distribution pattern is found in the closely related Teiidae of tropical America and the Lacertidae of the Old World (see Gorman, 1970, for references). Primitive teiids are in South America, and they apparently dispersed to North America by the Late Cretaceous (Estes, 1970; Savage, 1966). Kluge (1967) has argued that Africa and South America share closely related genera of the Gekkoninae and that South American forms do not appear to be derived from the north; he accounted for these similarities by rafting. Geckos are known from the Paleocene of Brazil (Estes, 1970), and these fossils are consistent with a long history in South America. The pythons and boas also probably had a common ancestor in a South American-African supercontinent. Little evidence seems to support derivation of boas from the north, but there undoubtedly has been dispersal of the family through the north (subfamily Ericinae). The two genera of boas on Madagascar, *Acrantophis* and *Sanzinia*, are apparently related to two separate New World genera *Eunectes* and *Corallus*, respectively (G. Underwood, pers. Comm.).

Among birds, the best example of a Gondwanaland Element is the ratites. The African ostrich (*Struthio*) and the South American rheas (*Rhea*, *Pterocnemia*) are each's sister-group, and their common ancestor must have inhabited a single continent (Cracraft, 1973 a, in press b). Other groups which were probably found in a Mesozoic supercontinent include cuckoos (Cuculidae), parrots (Psittacidae), pigeons (Columbidae), and suboscines (Cracraft, 1973 a); however, interfamilial relationships are still poorly known.

No Recent mammals can be inferred to have existed in a common South American-African continent. We can assume that protherians were undoubtedly present, and it would not be unexpected if fossil marsupials are eventually found in Africa (Fooden, 1972). I agree with Hoffstetter (1972) that the platyrrhine monkeys and caviomorph rodents of South America are probably related to the catarrhine monkeys and hystriomorph rodents of Africa, and that they most likely dispersed by rafting across the South Atlantic.

SOUTH AMERICA-AUSTRALIA

The available data suggest very strongly that a continuous land connection between Australia and South America was important for interchange of terrestrial vertebrate faunas. Certainly the amount of interchange was not anything like that between Africa and South America; nevertheless, it was considerably more than has been realized by many recent workers (Table 2).

TABLE 2. — Vertebrate taxa with probable sister-group relationships between South America and Australia¹

Taxon in South America	Taxon in Australia	Source of systematic data ²
<i>Fresh-water Fishes</i>		
Ceratodontidae	Ceratodontidae ³	a
Osteoglossidae (<i>Osteoglossum</i>)	Osteoglossidae (<i>Scleropages</i>)	e, b
<i>Amphibians</i>		
Hylidae	Hylidae	c, d
Leptodactylidae	Leptodactylidae	e
<i>Reptiles</i>		
Meiolanidae	Mriolanidae	f
Chelyidae	Chelyidae	f
<i>Birds</i>		
Struthionidae (<i>Rhea</i> + <i>Struthio</i>)	Casuariidae (<i>Casuaris</i> + <i>Dromiceius</i>)	g, h
All other ratites ⁴	Dromornithidae	g, h
All other galliforms (suborder Gallii)	Megapodiidae	g, i
Possibly some other suboscines ⁵	Menuridae, Ardeornithidae	g
Forpinae parrots	Platycecinne parrots	g, j
<i>Mammals</i>		
Prototheria ⁶	Prototheria	k
Metatheria	Metatheria	k, l

1. Includes only Recent families.

2. Abbreviations: a, Patterson, in press; b, Nelson, 1969b; c, Duellman, 1970; d, Tyler, 1971; e, Lynch, 1971; f, Darlington, 1957; g, Cracraft, 1973a; h, Cracraft, in press; i, Cracraft and Short, in press; j, Beccot, 1963; k, Foote, 1972; l, Tedford, in press.

3. Ancient group; very likely had marine ancestors (Patterson, in press).

4. Except for Diornithidae and Apterygidae (see Cracraft, in press b).

5. Specific group unknown; relationships very poorly known; Menurus may be related to oasian passerines.

6. Ancient group; unknown in South America; probably entered Australia from South America via East Antarctica.

Within fishes, dipnoans and osteoglossomorphs are known in both South America and Australia. Ceratodontid lungfishes were widespread at one time and are obviously relict in Australia. Patterson (in press) has argued that the most parsimonious hypothesis regarding ceratodontid evolution is that they were primitively a marine group. Thus, it may not be necessary to accept dispersal through fresh-water given present evidence. Nelson's (1969b) discussion of osteoglossomorph biogeography suggests the possibility of a close relationship between *Osteoglossum* of South America and *Scleropages*

of Australia and Southeast Asia. Nelson emphasizes the tentative nature of our phyletic knowledge, but I believe the evidence weighs in favor of a Southern Hemisphere interchange between the common ancestor of these two genera. The phyletic relationships as presently known and the distribution of these genera in fresh-water suggest that dispersal was through fresh-water. However, osteoglossomorphs were likely to have been primitively marine (Patterson, in press), and the presence of *Sceloporus* in Southeast Asia indicates the possibility of some marine dispersal.

Lynch (1971 : 206) has suggested that the cyclorhine leptodactylids of Australia and New Guinea may be the sister-group of the tropical American leptodactylids. I have maintained elsewhere (Cracraft, 1973 b) that if this is true, then transantarctic dispersal from South America is indicated. The same might be suggested for hylid frogs, although the relationships of the two genera in the Australo-Papuan region, *Litoria* and *Nyctimystes*, are as yet still in doubt (Tyler, 1971); some of these Australasian "hylids" may prove to be more closely related to the leptodactylids (Laurent, in press). Nevertheless, because hylids appear to have dispersed northward from a center of radiation in tropical America (Duellman, 1970), it would suggest the very real possibility of a South American origin for the family.

At the present time there is very little evidence supporting interchange in the reptile fauna between South America and Australia. Continuous land connections must have played a role in distributing turtles and crocodiles, but phyletic relationships are too poorly known to say exactly what this role was. The gekkonid subfamily Diplodactylinae is restricted to Australasia, and Kluge (1967 : 47) believes they originated from "the primitive gekkonid stock in the tropics of southeast Asia some time during the late Mesozoic." If Kluge is correct with the timing of this origin, then the ancestor would have had to disperse a considerable distance southward over water. Future studies on intergeneric relationships may suggest a southern origin for this subfamily.

The ratite birds provide one of the best examples of South America-Australia interchange (Cracraft, 1973 a, in press b). The Australo-Papuan family Casuariidae (cassowaries, emus) is the sister-group of the Struthionidae (South American rheas + African ostriches). Because of the Jurassic separation of Africa and Antarctica, it is most probable the ancestors of cassowaries and emus dispersed along a South American-East Antarctica-Australian route. Another family of extinct ratites, the Dromornithidae, are found only in Australia. Dromornithids are primitive ratites and apparently represent a separate invasion from the casuariids. The primitive galliform family Megapodiidae is restricted to Australia and the islands to the north. An analysis of their relationships to the other galliforms strongly indicates a Southern Hemisphere dispersal (Cracraft, 1973 a; Cracraft and Short, MS). The possibility exists that the forpne parrots of South America are closely related to the platycercines of Australia (Brereton, 1963) and, if this relationship can be verified, transantarctic dispersal would be suggested (Cracraft, 1973 a). The suboscines are also possibly a Southern Hemisphere group, and future studies may link the Australian Menuridae and Atrichornithidae with certain South American groups, but this is very tentative at this time. The menurids and atrichornithids may prove to be oscine passerines and not suboscines (Ames, 1971).

Within mammals, the prototherians and metatherians almost certainly entered Australia from the south (Fooden, 1972). Prototherians may have come either from South America or from Africa. Marsupials, on the other hand, in all probability came from South America, although the evidence is circumstantial (see Tedford, 1971, in press; Jardine and McKenzie, 1972).

In summary, there are several groups of vertebrates (leptodactylids, ratites, megapodes, marsupials) for which evidence of interchange between South America and Australia is strong. Other examples will almost certainly emerge as additional fossil material is recovered from both continents and as systematic data improve.

SOUTH AMERICA - NEW ZEALAND

Compared to that of Australia, the vertebrate fauna of New Zealand is rather limited in taxonomic and ecological diversity. There are no primary fresh-water fishes, only one group of frogs, a few

of reptiles, only a moderate number of avian endemics, and the sole native mammals are bats. No serious biogeographer can question the assumption that most of the vertebrate fauna of New Zealand arrived overwater. Nevertheless, some elements probably arrived from South America via West Antarctica.

The only amphibians on New Zealand are the endemic Leiopelmatidae. The species of *Leiopelma* are frequently included in the same family as those of *Ascaphus*, which are restricted to northwestern North America. At the present time, there is little evidence based on shared derived characters to support this convincingly, and an increasing number of herpetologists are beginning to question their relationship. Leiopelmatids are very primitive frogs and have no obvious affinities to other groups. The presence of other primitive frogs in South America (pipids) suggest the likelihood that leiopelmatids represent an early invasion to New Zealand from similarly primitive ancestors. All frogs in Australia are reasonably advanced, and none seem to be candidates for a possible sister-group of the leiopelmatids.

TABLE 3. — Vertebrate taxa showing probable sister-group relationships between South America and New Zealand¹

Taxon in South America	Taxon in New Zealand	Source of systematic data ²
<i>Fresh-water Fishes</i>		
None		—
<i>Amphibians</i>		
Primitive frogs ³	Leiopelmatidae	—
<i>Reptiles</i>		
Sphenodontidae ⁴	Sphenodontidae	—
<i>Birds</i>		
All other ratites (infraorder Struthionae)	Dinornithidae-Apterygidae (infraorder Apteryges)	a, b
Spheniscidae	Spheniscidae	a, c
Some other suboscines ⁵	Acanthiittidae	a
<i>Mammals</i>		
None	—	—

1. Includes only Recent taxa [except for penguins; see text].

2. Abbreviations: a, Cracraft 1973a; b, Cracraft, in press b; c, Simpson, 1974.

3. Specific group unknown; leiopelmatids most likely entered New Zealand from South America via West Antarctica.

4. Ancient group; unknown in South America but widespread elsewhere in Mesozoic; most likely entered New Zealand from South America via West Antarctica (see text).

5. Specific group unknown; interrelationships very poorly known.

The two endemic genera of geckos, *Hoplodactylus* and *Naultinus*, are members of the Australasian subfamily Diplodactylinae and probably arrived overwater from the Australian region. The Tuatara (*Sphenodon*) is clearly a relict of a very ancient group that was once broadly distributed over much of the world. It is probable they arrived in New Zealand from South America via West Antarctica, but this will only be demonstrated by identifying the South American sister-group. All other reptiles, scincids, marine turtles, and snakes, very probably arrived overwater and no evidence exists for terrestrial dispersal.

The best documented example of a Gondwanaland Element in New Zealand's fauna is the ratite birds (Cracraft, 1973 a, in press b). The moas (Dinornithidae) and kiwis (Apterygidae) form a monophyletic assemblage (infraorder Apteryges) of species whose sister-group is the other ratites (infraorder Struthionis). Since they are not the sister-group of the emus and cassowaries of Australia, they undoubtedly represent a separate invasion across West Antarctica from South America. No other vertebrate taxa can be specifically linked phylogenetically with a group in South America, although there are some distinct possibilities. Late Eocene-early Oligocene penguins of New Zealand show a remarkable similarity to a fauna of approximately the same age on Seymour Island (Simpson, 1971), and this is most economically explained by the close proximity of the lands through West Antarctica (Cracraft, 1973 a). The suboscine passerine family, Acanthisittidae, of New Zealand may have a close relationship to some suboscine group in South America, but this is not yet proven (Cracraft, 1973 a). There is little doubt that most New Zealand birds arrived via overwater dispersal.

AUSTRALIA-NEW ZEALAND

To my knowledge, Australia and New Zealand do not share any vertebrate taxa whose sister-group relationships are sufficiently old to have been in existence prior to the breakup of Gondwanaland. *Leiopelma*, as noted above, does not appear closely related to any known frog in Australia. Rhynechocephalians are as yet unknown from Australia, although it is difficult not to believe they once were living there. New Zealand geckos probably arrived overwater from Australia. Australia was clearly a prime source for New Zealand's birds. Australia's ratites are phylogenetically close to rheas/ostriches, not moas/kiwis. Perhaps Australia's suboscines (Menuridae, Atrichornithidae) shared a common ancestor with the New Zealand Acanthisittidae, but no evidence exists for this at present; if they are related, dispersal was probably overwater. No land mammals are shared, although prototherians, and to a lesser extent marsupials, might be expected in New Zealand if the proper deposits were available.

To summarize, except for those groups classified as overwater Cenozoic derivations, New Zealand shows no confirmed relationships in the vertebrate fauna to Australia.

AFRICA-AUSTRALASIA

Africa shares a number of families (or superfamilial taxa) with Australasia, and nearly all of these similarities are with Australia (Darlington, 1957). Distributional and evolutionary patterns are also clear in showing that most of these similarities are the result of a common fauna extending through tropical Asia and the Indo-Australian Archipelago. Whereas it seems fairly certain that Australia and Africa share elements of a Gondwanaland fauna, almost no support can be given for the hypothesis that this element in Australia arrived directly from Africa via Antarctica rather than from South America.

Among fresh-water fishes, Africa and Australia share lungfish (Dipnoi) and osteoglossomorphs. The Australian lungfishes (Ceratodontidae) are relicts of a marine group that was nearly worldwide in the Mesozoic. Osteoglossomorphs also are, or were, broadly distributed (Nelson, 1969 b). It is probable that both groups entered Australia from the south (dipnoans possibly from the sea), but there is nothing to suggest a close relationship to African representatives. The available information tends to favor relationships between the osteoglossomorphs of Australia and South America.

Most frogs of Australia probably entered from the north, including the microhylids (but see above) and ranids. The Hylidae are not shared with Africa. The helophrynine leptodactylids of Africa are among the most primitive members of the family as are the myobatrachines of Australia. However, it is almost certain that the latter group entered Australia from the north (Lynch, 1971; Cracraft, 1973 b).

Nearly all of the shared reptile families of Australia and Africa are widely distributed in the

Old World, and most undoubtedly entered Australia from the north. Of the probable Gondwanaland Element among reptiles (agamids, geckos, boids), these too undoubtedly dispersed through the Indo-Australian islands.

Dispersal through Southeast Asia also explains similarities of the avifaunas. Although rattes and megapodes are southern groups, they do not share sister-groups between Australia and Africa, and movement was from South America. The majority of Australasian birds, including all the passerines, clearly dispersed southward from Southeast Asia (Mayr, 1944; Cracraft, 1972 b, 1973 a).

No land mammals other than muroid rodents are shared between Australia and Africa (Keast, 1969). Muroids entered Australia from the north.

In summary, no sister-group relationships have been demonstrated that would suggest Africa and Australia at one time exchanged vertebrates directly via Antarctica. Only chelonians, rhynchocephalians, crocodylians, and other primitive reptiles and amphibians are probably sufficiently old to show this pattern, but relationships are poorly known among these groups.

DISCUSSION

ANTARCTICA AS A FAUNAL DISPERSAL ROUTE : PALEOGEOGRAPHIC CONSIDERATIONS

The paleogeographic and biological data discussed above offer a basis for reconsideration of the role of Antarctica in Southern Hemisphere vertebrate dispersal. Most workers now accept the fact that temperate forests were present intermittently on Antarctica until the end of the Miocene (evidence reviewed in Cracraft, 1973 a), hence a climate conducive to a varied vertebrate fauna is no longer an issue. Nevertheless, many biologists question whether Antarctica played a significant role in the dispersal of Recent vertebrates (Simpson, 1940; Darlington, 1965 : 156-158; Keast, 1971 : 356). There seem to be a number of reasons for this conclusion. First, many workers did not accept the geological evidence supporting land connections (especially by elaborate land bridges) of Australia, New Zealand, and South America to Antarctica in the Cretaceous and early Tertiary. There are ample data now to lay this objection to rest. Second, incorrect or inadequate information regarding phylogenetic relationships led some biologists to reject valid faunal similarities between the southern continents. And third, several biogeographers have found it difficult to accept the presence of a number of land vertebrates on Australia but relatively few on New Zealand. This view was held as early as the first part of this century when Hedley (1912 : 87) stated : "Clearly the Antarctica that supplied Australia with an abundant fauna of marsupials, monotremes, snakes, frogs, and so on, was not in touch with New Zealand, where these animals are conspicuously absent". Darlington (1965 : 106) believes it is "difficult to credit a land bridge that would be crossed by birds [moose] on foot but not by other contemporaneous land vertebrates." And Keast (1971 : 360) notes that for "New Zealand to have acquired rattes but not the equally old, or older, mammals is anomalous." Thus, one of the major unresolved problems of Southern Hemisphere biogeography is why New Zealand did not share some of the faunal elements that were presumably dispersing to Australia. Keast (1971 : 360) offers possible reasons such as differences in the times of breakup of New Zealand and Australia and secondary extinction. These explanations are distinct possibilities and probably of some importance, but the major reason may lie with the markedly different paleogeographic histories of East and West Antarctic (see Hamilton, 1967; Craddock, 1970; Elliot, 1972). East Antarctica is formed by a large Precambrian shield that has remained relatively intact throughout the Mesozoic and Cenozoic. By contrast, West Antarctica is composed of younger (Paleozoic) rocks that have been greatly deformed and intruded by igneous rocks during the Mesozoic and Cenozoic. If one examines a map of subglacial Antarctica (Fig. 5), it is clear that most of East Antarctica would be above sealevel after removal of

the ice and isostatic rise of the land (Hamilton, 1967). West Antarctica, on the other hand, would be a series of mountainous islands separated by deep trenches. It can be reasonably inferred that this topographical picture prevailed immediately prior to glaciation, but it is not at all certain what West Antarctica was like in the late Mesozoic and early Tertiary. Plate tectonic theory would seem to imply that when the New Zealand and West Antarctica (Marie Byrd Land) continental blocks were joined, subaerial land was much more widespread. It is only after rifting that one would expect subsidence of the continental margins.

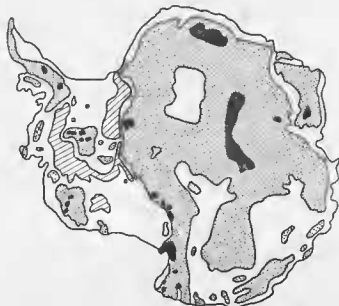


FIG. 5. — Approximate topography of Antarctica with pack ice removed and after isostatic rise of the land. Note particularly the interruption of land in West Antarctica (left) compared to continuous land in East Antarctica (right). A number of regions are still insufficiently known. Dark areas, above 2000 meters; dotted areas, 0 to 2000 meters; clear areas, 0 to -1000 meters; lined areas, below -1000 meters.

A continuous broad continental shield between East Antarctica and Australia does much to explain the fairly substantial vertebrate fauna that reached the latter continent. It is now generally accepted that considerable movement was taking place among the land masses of West Antarctica in the late Mesozoic and early Cenozoic (see Hamilton, 1967; Schopf, 1969; Elliot, 1972). A continuous land connection between the Antarctic Peninsula (which was part of South America), the remaining land of West Antarctica, and New Zealand must be considered problematical and intermittent at best. I believe, therefore, that the paucity of terrestrial vertebrates and fishes in New Zealand can be explained by the relatively short periods of time that continuous land was available for dispersal. The presence of ratites, leiopelmatid frogs, and *Sphenodon*, while not constituting proof, suggest that land connections were at least occasionally available, and if one assumes that such routes were infrequent (as the geological evidence indicates), then it would readily account for the absence of a more diverse fauna. Very probably, the fact that New Zealand separated from West Antarctica in the Late Cretaceous also did much to keep many of the younger vertebrate taxa from reaching the islands.

The differences in the ratites, frogs, and some insects between New Zealand and Australia can be explained by evolution in isolation after continental breakup but perhaps also by the dispersal barrier formed by the Transantarctic Mountains separating East and West Antarctica. Thus, as shown in Fig. 6, vertebrates entering Antarctica from South America either went across West Antarctica to New Zealand or across East Antarctica to Australia. There is no evidence to suggest that animals were able to disperse overland between Australia and New Zealand, hence it is probable that even

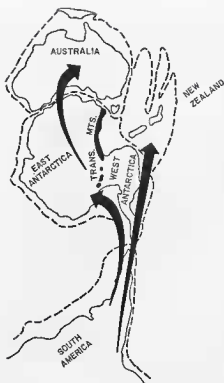


FIG. 6. — Probable dispersal routes (arrows) around the southern end of the world in the late Cretaceous prior to 80 m.y. Present continental outlines are joined at approximate boundaries of continental crust. The Andean Cordillera-Antarctic Peninsula contact is straightened according to Dalziel and Elliot (1974) and New Zealand is fitted according to Griffiths (1971). The Transantarctic Mountains, which were possibly a barrier between East and West Antarctica, are shown in black. See text and figure 5.

prior to drift some water barriers very probably were present. Future discoveries of fossil vertebrates on New Zealand may either confirm or deny this assumption, as also might dating of the ocean floor in the southwest Pacific. At least the vertebrates do not suggest this interchange.

The width of the land connection between South America and East Antarctica is unknown, but it might be assumed that a fairly narrow corridor would have functioned as a filter to various faunal elements. Presumably, a narrow land connection coupled with the more rigorous ecological conditions of high latitudes explain the reduction in faunal interchange that is apparent between Australia and South America as compared to Africa and South America. By the Late Cretaceous or early Tertiary the Antarctic Peninsula-Andean Cordillera was being fragmented and pushed eastward, and it can be expected that vertebrate dispersal became more "sweepstakes" in character.

VERTEBRATE DISPERSAL PATTERNS AND
COMPARISONS WITH INVERTEBRATES

The patterns of vertebrates dispersal in the Southern Hemisphere are beginning to emerge and seem consistent with our knowledge of continental history. The broad connection between South America and Africa, in the presence of tropical conditions, allowed a similar and diverse fauna to evolve in both areas prior to breakup. Connections of Australia and New Zealand to Antarctica enabled them to receive immigrants from South America. However, various kinds of barriers appear to have greatly reduced or eliminated interchange between Australia and New Zealand. The early separation of Africa from Antarctica precluded interchange between the faunas of Africa and Australia except by way of South America or Southeast Asia. If these are indeed the major vertebrate dispersal patterns of the late Mesozoic and early Cenozoic, how do they compare with those of the invertebrates?

Brundin (1965, 1966, 1970) has presented the most elegant analysis of Southern Hemisphere biogeography for any group of invertebrates. Studying chironomid midges, he was able to demonstrate numerous examples of phylogenetic relationships between midges in South America and those in New Zealand and Australia but not between the latter two continents. Because Brundin was concerned only with the midge fauna of southern Africa, it was not possible to show extensive relationships between Africa and South America. The biogeographic patterns of the chironomid midges are consistent with those of the vertebrates.

Keast (1973) has reviewed the extensive literature on invertebrate distribution in the Southern Hemisphere. In those cases in which systematics are fairly reliable, the following patterns seem evident:

a. The close relationships between the faunas of Australia and South America is obvious. A number of families in the following orders of insects are shared between these two areas: Plecoptera, Megaloptera, Hemiptera, Odonata, Orthoptera, Coleoptera, Trichoptera, and Hymenoptera. In addition, many families of insects share genera between Australia and South America.

b. The temperate invertebrate faunas of South Africa are fairly distinct from the same faunas on the other southern continents. At the present time a major gap in our knowledge is the lack of comparative analysis of the tropical portions of Africa and South America. It can be expected that this will yield a large number of groups in common between these two areas.

c. The invertebrate faunas of Australia and New Zealand "are relatively distinct and this could be consistent with the earlier isolation of the latter as indicated by the geological data" (Keast, 1973).

These invertebrate patterns, then, seem to parallel those of the vertebrates.

THE BREAKUP OF GONDWANALAND AND THE
RELATIVE AGES OF SOUTHERN FAUNAS

The sequence of breakup and dispersal of the Gondwana landmasses discussed earlier has been of some importance in determining the relative ages of the faunal elements shared between any two continents. The Jurassic separation of Africa and Antarctica assured that only the early Mesozoic faunal elements of Africa would be shared with Antarctica and Australia (thus little or no direct dispersal of late Mesozoic faunas of Africa has taken place via Antarctica). The most likely groups showing Africa-Antarctica-Australia similarities might be early Mesozoic amphibians and reptiles (see Colbert, 1974), lungfish, and the still extant rhynchocephalians. Almost no young groups are involved unless via Southeast Asia.

The middle Cretaceous separation of Africa and South America resulted in only the more ancient families being shared and in the sharing of sister-group families that were each differentiated in isolation on the two continents. Most of the shared families are fishes and amphibians, whereas reptiles and birds mainly share sister-group families. Seemingly, this reflects the older age of the former two groups.

The age of the Gondwana vertebrate fauna of New Zealand also reflects the Mesozoic date of separation. Rhynchocephalians, leiolopids, and moas-kiwis are all very primitive within their respective groups.

Finally, the relatively later separation of Australia resulted in a somewhat younger fauna. Most of the frogs are in the same families as those of South America, the lizards (possibly geckos) are too, as are some (but not all) of the birds.

Parallel age differences in the invertebrate faunas as they relate to the separation sequences of the continents are discussed by Keast (1973).

THE BREAKUP OF GONDWANALAND AND THE EVOLUTION OF TAXONOMIC DIVERSITY

It has been suggested by Kurten (1969) that the breakup of Gondwanaland enabled the evolution of similar ecological types in different taxonomic groups on each of the isolated continents. This, he maintains, partially accounts for the increase in taxonomic diversity between the Mesozoic reptiles and Cenozoic mammals. I do not believe there can be any question that the fragmentation of Gondwanaland increased the diversity among the higher categories of Recent vertebrates. The opening of the South Atlantic apparently increased suprageneric diversity in fishes (especially siluriforms), frogs (leptodaetylids, bufonids), snakes (boas, pythons), lizards (teiids, lacertids), and birds (rhea, ostrich). The isolation of Australia and New Zealand also resulted in the differentiation unique groups vertebrates on those continents. As more detailed studies of individual families inhabiting the southern continents are completed, many additional examples will undoubtedly be found.

ADDENDUM

In view of the fact that this paper has been *in press* since late 1972, I want to call attention to a number of recent papers that pertain to some issues I have discussed above.

South America-Antarctica. As noted earlier, the Andean Cordillera-Antarctic Peninsula was disrupted in the Cenozoic. However, this linear cordillera was uplifted in the early late Cretaceous and oroclinal bending took place earlier (Dalziel, I. W. D., et al., 1973. Pp. 87-101 in *Implications of Continental Drift to the Earth Sciences*, ed. by D. H. Tarling and S. K. Runcorn. London: Academic Press). Thus, it is difficult to say much about the precise nature of the connections between South America and East and West Antarctica in the Cretaceous. The corridor may have been continuous at times (especially to East Antarctica), archipelagic at others. Before spreading began in the Scotia Sea area, parts of the region that are now continental shelf may have been subaerial.

Australia. The discovery of an older magnetic anomaly now dates the time of onset of drift between Australia and East Antarctica at about 55 m.y. ago (Weissel, J. F. and D. E. Hayes, 1972. *Antarctic Res. Ser.* 19: 165-96). This new estimate of the time of drift does not affect any of the biogeographic conclusions of this paper.

Biogeography. Two books have appeared that contain papers about vertebrates of the Southern Hemisphere. The first, *Evolution, Mammals, and Southern Continents* (Albany: State University of New York Press, 1972), includes discussions about the origin and evolution of the mammalian faunas of South America, Africa, and Australia. The second, *Evolutionary Biology of the Anurans* (Columbia: University of Missouri Press, 1973), presents up-to-date opinions on relationships of frogs and their biogeography. Clearly, there is still great controversy about the phylogeny of frogs, and thus their biogeography must remain tentative.

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DISCUSSION

Intervention du Professeur R. Hoffstetter.

La documentation réunie par M. Cracraft est remarquable et je l'en félicite. Peut-être, cependant, se montre-t-il un peu trop optimiste, en ce qui concerne sa « théorie biogéographique ». Pour ma part, je reste sceptique sur les informations que l'on peut tirer de la distribution *actuelle* d'un taxon, tant pour le lieu d'origine et l'histoire biogéographique de ce taxon, que pour la localisation de son groupe frère. On pourrait citer notamment bien des exceptions au postulat qui veut que la forme « ancestrale » occupe une position centrale et les formes dérivées des positions marginales dans l'aire de distribution d'un groupe. M. Cracraft lui-même souligne que les éléments de la faune néozélandaise (Rhynchocephales, Leiopelmidés, Kiwis) sont très primitifs dans leurs groupes respectifs : je ne crois pas qu'il veuille en conclure que ces groupes ont leur berceau en Nouvelle-Zélande !

Certes la paléontologie présente trop de lacunes pour permettre, dans tous les cas et en toute certitude, la reconstitution d'une histoire paléogéographique. Elle apporte cependant des éléments dont il convient de tenir compte. Ainsi, pratiquement tous les Agamidés fossiles (y compris le plus ancien, *Euposaurus*, du Jurassique supérieur) proviennent de la Laurasie ; il est donc difficile de conclure qu'il s'agit probablement d'un groupe gondwanien ! En ce qui concerne les Tégiidés, leurs représentants les plus anciens proviennent du Crétacé supérieur nord-américain ; il semble qu'ils s'éteignent ensuite localement ; mais on les retrouve en Amérique du Sud, où ils sont attestés depuis le Paléocène ; ils ne réapparaissent en Amérique du Nord que dans le Tertiaire supérieur ; en attendant de nouvelles découvertes, la prudence voudrait que l'on s'en tînt provisoirement à ce schéma concret, plutôt que de supposer un berceau hypothétique en Amérique du Sud.

Réponse du Professeur Cracraft au Professeur R. Hoffstetter.

The theory of biogeography that I advocate is deductive in form, that is, biogeography is deduced from some concept of phylogenetic relationships. The reasoning that has been proposed by Brundin, Nelson, and others has a logical structure such that *phyletically* primitive taxa will tend to be located at the center of origin of the group as a whole (simply because the center of origin is deduced from the phylogeny). This does not imply that "primitive" taxa cannot be distributed otherwise, only that one must have some phyletic evidence to show this (this issue is discussed in detail in a separate paper, "The Theory of Historical Biogeography,").

I place less emphasis on the fossil record as an indicator of centers of origin than I do on phyletic patterns. I agree that the situation with the Agamidae is equivocal, but patterns within the Teiidae and their relationship to Lacertids do not support a Laurasian origin.

Intervention du Professeur A. Simonetta

I shall like to know whether you have any new positive evidence for a monophyletic origin of the ratites. I am not aware of any convincing evidence for it and, as far as I can see from personal work on the skull morphology of the birds, *Rhea* seems to be related to the Tinamus and the Acipornithidae are close to the Ostrich.

Réponse du Professeur Cracraft au Professeur Simonetta.

I have presented elsewhere (*Ibis*, in press) a re-evaluation of ratite phylogeny. The ratites and tinamous share several derived characteristics that support their monophyly : (1) the palaeognathous palate (Bock, W. J. 1963. *Proc. 13th Intern. Ornithol. Congr.* : 39-54), (2) rhamphothecal structure (Parkes, K.C., G.A. Clark, Jr. 1966. *Condor* 68 : 459-71), (3) and pelvic structure (Cracraft, *Ibis*, in press).

Intervention du Professeur P. G. Martin

Since Dr. Cracraft places some emphasis on the reconstruction of Griffiths, I wish to draw attention to two relevant lines of geophysical evidence which that author did not discuss.

Ringis (1970) (*Geoexploration* 8, p. 250) has found a magnetic anomaly pattern in the Tasman sea trending N 30°W, i.e. about 45° to the adjacent coast of New South Wales. Ringis was unable to correlate these reversals with the reversal pattern up to 80 M.Y.B.P. and suggested that they were older. If he was correct, the Tasman sea must be at least 110 M.Y. old (since between 80 and 110 M.Y.B.P. there was a magnetically stable period) and Griffith's reconstruction for 80 M.Y.B.P. must be wrong.

Griffiths reasonably used the analysis of the Endeavour Fracture Zone (Christoffel and Ross (1970) *Earth & Planetary Sci. Letters* 8, 125 p.) to place the New Zealand platform against Marie Byrd Land at 80 M.Y.B.P. However, he ignored the Cretaceous magnetic pole for Marie Byrd Land (Schoron et al. (1970) *Antarctic J. of the U.S.S.*, p. 219) which is at 105°E, 30°S and suggests that New Zealand plus Marie Byrd Land were not only far to the North in the Pacific but nearer to South America than to Australia.

Réponse du Professeur Cracraft au Professeur Martin.

Hayes and Ringis (1973. *Nature*, 243 : 454-58) have shown that the Tasman Sea was formed between 60-80 m.y. ago. Their study is reasonably consistent with the reconstruction of Griffiths. Clearly, however, our ideas about the geophysical history of New Zealand and West Antarctica are very tentative, and it very well may be that there has been some relative movement between the New Zealand-West Antarctic block and East Antarctica.

Intervention du Professeur R. F. Laurent

The Australian so called hylids are probably not hylids at all, but a parallel offshoot of the local cycloranines or myobatrachines. After all, the reason why Australian tree frogs and South American tree frogs have been classified together is that both are arboreal! Caryologically, Dr Morrisspolhi detected relationships between the Australian tree frogs and the sympatric leptodactylids.

Réponse du Professeur Cracraft au Professeur Laurent :

I noted in my paper that the relationships of these Australian frogs are uncertain. To my knowledge, conclusive evidence has yet to be presented. If they do have relationships to hylids and/or leptodactylids (or to cycloranines which are probably related to one or the other of these families), then some trans-Antarctic distribution pattern seems likely.